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DISTRIBUTED MODELLING OF DETERMINISTIC AND STOCHASTIC POPULATION DYNAMICS

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Abstract—In many problems of practical purpose, one is interested not only in the study of the total population of the overall system, but also in the distribution of the population depending upon some characteristic parameters. This necessity is patent in biological systems defined on a wide range of distributed features, but it is also in order when one tries to analyze social systems by means of population models. As a matter of fact, with this objective in mind, we deal with infinite species population models.

This study discusses this question, proposes a distributed version for the logistic equation, and examines the existence of stationary solutions. The problem of the influence of environmental noise on the dynamics of the distributed population is considered, and a model is proposed. A detailed analysis is carried out around the stationary solution via a linearization technique, and the covariance equation is derived.

1. INTRODUCTION

The study of population models is mainly centered around the equation

$$\dot{p} = ap - bp^2,$$

known as the logistic law or population law, and which was first introduced in 1837 by the Dutch mathematical-biologist Verhulst. In this equation, $p = p(t)$ denotes the size of the population of a given species at time t, a is the constant of the Malthusian law of population growth $\dot{p} = ap$, and bp^2, with b constant, is the competition term which reflects the fact that individual members are competing with each other for the limited living space, natural resources, and available food.

This equation has been the subject of a considerable amount of literature (see, for instance, [1]) and was mainly considered in more complete forms by introducing time lag (see, for instance, [2]) or random parameters in the environment (see, for instance, [3, 4]).

Basically, the individuals are indexed by a distributed parameter z, for instance the age, and the above equation defines the dynamics of the population as a whole, irrespective of its distribution *w.r.t.z*. Nevertheless, in a large number of cases, it appears that it is interesting to have not only the dynamics of the whole population, but also its distribution with respect to z. This need is patent, for instance, when one tries to use population models to analyze social systems in which the distribution over the social strata is of major importance. One may, of course, consider a social system as a multispecies pop-

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ulation model; but at a certain level of aggregation, the system can be considered as involving an infinite number of species, therefore it is a distributed one.

In this study, we shall present a rather detailed derivation of a class of distributed population models in both the deterministic case and the stochastic one, along with some discussion of the qualitative properties of these models. The problem of the stationary states is examined and estimates are given. The effects of random environmental fluctuations on the dynamics of the population are analyzed via a linearization technique around the deterministic stationary state and the equation of the covariance function is derived.

2. A CLASS OF POPULATION MODELS WITH INTRA-SPECIES COMPETITIONS

2.1. *Preliminary considerations*

The state of a dynamical system S is generally denoted by $x(t, z)) \in \mathbb{R}^n$, where $t \in \mathbb{R}^+$ is the time, and where z is a real valued vector parameter which characterizes the physical properties of the objects under consideration, which make up the system S. For instance, x may be the number of people with a given income z or else the number of insects with the age z.

The dynamics of S is usually defined by a balance condition in the form of the differential equation

$$\dot{x}(t, z) = E(\cdot)\cdot x(t, z), \tag{2.1}$$

where $E(\cdot)$ denotes an operator referred to as an *evolution operator*. This equation involves a broad class of systems such as physical processes, biological systems, economic models, and social systems, to mention only these ones.

In a very large number of cases, the equation

$$E(\cdot)\cdot x(t, z) = 0 \tag{2.2}$$

has solutions different from the trivial one, and, in addition, these solutions are stable, a property which results from the fact that if a system is observable in the broad sense of this term, then its characteristics should be repeatedly measurable, a feature which implies some properties of stability. As a result, the operator $E(\cdot)$ *is generally nonlinear*.

The parameter z itself may depend upon time following a differential equation like

$$\dot{z} = \Psi(x, \xi, t, z, u), \tag{2.3}$$

where ξ denotes an environmental parameter, for instance a disturbing noise, and u is a control vector, or a regulation vector, if we refer to cybernetic systems which converge to a self-organizing state.

As a matter of fact, x may depend upon a distributed spatial parameter, so that, in the general case, Eq. (2.1) should be a partial differential one. But in a first practical approach, the use of finite difference schemes converts the distributed system into a lumped one, so that we can restrict the study to that of Eq. (2.1).

2.2. *Systems with unvarying characteristics*

We now consider the special case in which x and z are scalar, and is time unvarying. Explicitly, $x(t, z)$ represents the number of elements, say of biological units for fixing the thought, which at the instant t have the property z. We shall write the dynamics of the evolution in the form

$$E(\cdot)\cdot x = A\cdot x - B\cdot x, \tag{2.4}$$

where A denotes a birth rate operator, and B is the death rate one. Let $a(t, z, s)$ denote the total number of the individuals endowed with the property z and which are born from an individual having the property s; and let Z denote the maximum value of z; $0 \leq z \leq Z$. Then, one has

$$A\cdot x = \int_0^Z a(t, z, s)x(t,s)\,\mathrm{d}s. \tag{2.5}$$

In its more general form, the death-rate operator may be written as a nonlinear transformation

$$B\cdot x(t, z) := \mathrm{d}(t, x, z)x, \tag{2.6}$$

and we shall decompose $\mathrm{d}(t, x, z)$ into the form

$$\mathrm{d}(t, x, z) := b(t, z) + \int_0^Z r(t, z, s)x(t, s)\,\mathrm{d}s, \tag{2.7}$$

where $b(t, z)$ denotes the natural death-rate coefficient, and the integral term represents the death-rate effect which results from intra-species competition between individuals having different properties.

We then have the final dynamics

$$x(t, z) = \int_0^Z a(t, z, s)x(t, s)\,\mathrm{d}s - [b(t, z) + \int_0^Z r(t, z, s)x(t, s)]x(t, z) \tag{2.8a}$$

with the initial condition

$$x(0, z) = x_0\,(z) \tag{2.8b}$$

2.3. *Systems with time-varying characteristics*

Again we assume that x and z are scalar, but z depends explicity upon t, say $z(t)$. In such a case, we have the equation

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z}\dot{z} = E(\cdot)\cdot x. \tag{2.9}$$

The solution of this partial differential equation is defined by its initial condition, that is to say Eq. (2.8b), but also by its boundary condition, that is here, the relationship for $z = 0$. We shall write it in the form

$$x(t, 0) = \int_0^Z a(t, x)x(t, s)\,\mathrm{d}s, \tag{2.10a}$$

the meaning of which is obvious: for instance, assuming that z denotes the age, then it represents conditions resulting in births, and $a(t, s)$ is a birth-rate coefficient.

We shall write the explicit form of Eq. (2.9) as

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z}\dot{z} = -[b(t, z) + \int_0^Z r(t, z, s)x(t, s)\,\mathrm{d}s]x(t, z), \tag{2.10b}$$

with the initial condition

$$x(0, z) = x_0(z). \tag{2.10c}$$

In the special case where $\dot{z} = 1$, we then have

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z} = -[b(t, z) + \int_0^Z r(t, z, s)x(t, x)]x(t, z), \tag{2.11}$$

which is a generalized form of the transport equation

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z} = -b(t, z)x(t, z). \tag{2.12}$$

2.4. *On the meaning of these models*

(i) When $r \equiv 0$, Eq. (2.7a) reduces to

$$\dot{x}(t, z) = \int_0^Z a(t, z, s)x(t, s)\,\mathrm{d}s - b(t, z)x(t, z)$$

which is quite equivalent to the well-known dynamics referred to as the master equation by physicists or the Mathusian equation by biologists. More explicitly, if we consider the general case in which the system is described by discrete variables which can be lumped together to a vector m, then the probability $p(m, t)$ of finding the system in the state m at the instant t is defined by the equation

$$\dot{p}(m, t) = \text{rate in} - \text{rate out}.$$

Let $q(m, m')$ denote the transition probability per unit time that the system pass from m' to m, then we obtain

$$\text{rate in} = \sum_{m'} q(m, m')p(m', t)$$

and

$$\text{rate out} = p(m, t)\sum_{m'} q(m', m).$$

(ii) The intra-species competition term defined by the integral which contains $r(\cdot)$ in Eq. (2.7a) may be derived as follows.

Assume that we have three classes s_1, s_2, and z. The number of individuals of the class z which die at time t because of the competition with the elements of the class s_1 may be written in the form $k_1x(t, z)$; likewise for the effect of the class s_2, so that the total number of dead elements is $(k_1 + k_2)x(t, z)$. This being so, k_i should depend upon $x(t, s_i)$; more explicitly, it is an increasing function of $x(t, s_i)$, and in addition, it should depend upon the pair (s_i, z) to picture the fact that the grade of competition is a function of the two classes under consideration. Likewise, in the most general case, one may assume that the grade of competition is time varying, that is to say, that k_i is an explicit function of time.

A simple model which complies with these requirements is $k_i := r(t, z, s_i))z(t, s_i)$, therefore the number of dead elements is

$$[r(t, z, s_1)x(t, s_1) + r(t, z, s_2)x(t, s_2)]x(t, z).$$

Applying these arguments to continuous parameters is direct.

(iii) Basically, $a(t, z)$ in the expression (2.5) is the outcome of a stochastic process whose the greatest probability corresponds to $z = s$ in the most general case. In a biological framework for instance, $a(t, z)$ is defined by Mendel's laws and by mutation probabilities.

(iv) The function $r(t, z, s)$ is a deterministic function which is related to the grade of competition between the classes z and s and it clearly exhibits a maximum. Generally, in biological systems, this maximum is reached for $z = s$, but we may have different situations in economic systems or societal systems, for instance.

(v) The deterministic function $r(t, z, s)$ characterizes, for instance, the adaptation properties of individuals to the environment in the presence of limited resources. In this way, it pictures a natural selection of the Darwinian type.

Assume that z refers to the age of the biological units; then $r < 0$ describes the effects of mutual assistance between the different ages.

3. DISTRIBUTED MODELS WITH HEREDITARY EFFECTS

In more realistic systems, the dynamics is unavoidably affected by some time lags. For instance, in an actual ecosystem, the resource that the population $x(t, z)$ feeds on is replenished but the amount of disposeable resource at t depends upon the distribution of the population at $t - \tau$, say $x(t - \tau, z)$. This time lag affects directly the competing term rx, so that Eq. (2.7a) becomes the delayed one

$$\dot{x}(t, z) = \int_0^Z a(t, z, s)x(t, s)\,\mathrm{d}s - [b(t, z) + \int_0^Z r(t, z, s)x(t - \tau, s)\,\mathrm{d}s]x(t, z), \quad (3.1)$$

and Eq. (2.9b) is replaced by

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z}\dot{z} = -[b(t, z) + \int_0^Z r(t, z, s)x(t - \tau, s)\,\mathrm{d}s]x(t, z), \quad (3.2a)$$

with the initial condition

$$x(t, z) = \tilde{x}(t, z), 0 \leq t \leq \tau. \quad (3.2b)$$

4. DISTRIBUTED MODELS WITH RANDOM EFFECTS

4.1. *General considerations*

A problem of interest is the analysis of the influence of environmental random fluctuations on the dynamics of $x(t, z)$; like for instance, fluctuations in weather or resources.

The most direct idea is to introduce random noises in the different deterministic equations we derived above, as perturbations in the structural parameters of the population.

The problem of defining distributed random noises gives rise to a considerable amount of theoretical difficulties of a mathematical nature, and here, in our applied directed approach, we shall merely consider a practical modelling which is rather related to the engineering and physics framework.

In fact, the basic question is to define which calculus, from that of Stratanovich or of Ito, is the most appropriate for the model.

Turelli[5] discussed this question and proposed criteria to determine the appropriate calculus for the situation which is being modelled. As a result, if we consider environmental noise which is actually noncorrelated, Ito's formalism is best suited for our purpose.

4.2. *A few prerequisites*

We consider the vector stochastic differential equation in Ito's sense, which is

$$dx_t = f(x_t, t)\, dt + G(x_t, t)\, d\beta_t, \tag{4.1}$$

where x_t and f are n-vectors, G is an $n \times m$ matrix, and β_t is a vector of m independent Brownian notions, each with a unit variance parameter. We use the norms

$$|x| := \left(\sum_1^n x_i^2\right)^{1/2} = (x^t x)^{1/2} \tag{4.2}$$

$$|G| := \left(\sum_{i=1}^n \sum_{j=1}^m G_{ij}^2\right)^{1/2} = [tr(GG')]. \tag{4.3}$$

It can be shown[6] that if:

(i) There is a $K > 0$ such that

$$|f(x, t)| \le K(1 + |x|^2)^{1/2}$$
$$|g(x, t)| \le K(1 + |x|^2)^{1/2};$$

(ii) f and g satisfy uniform Lipschitz conditions in x:

$$|f(x_2, t) - f(x_1, t)| \le K|x_2 - x_1|,$$
$$|g(x_2, t) - g(x_1, t)| \le K|x_2 - x_1|;$$

(iii) f and g satisfy the uniform Lipschitz condition in t on (t_0, T):

$$|f(x, t_2) - f(x, t_1) \quad| \le K|t_2 - t_1|$$
$$|g(x, t_2) - g(x, t_1)| \le K|t_2 - t_1|;$$

(iv) x_{t_0} is any random variable with $E\{|x_{t0}|^2\} < \infty$ independent of $[d\beta_t, t \in [t_0, T]\}$;

Then Eq. (4.1) has a continuous solution in the mean square sense. $E\{x_t^2\}$ is bounded, $x_t - x_{t_0}$ is independent of $\{d\beta_\tau, \tau \ge t\}$ for every $t \in [t_0, T]$; $\{x_t\}$ is a Markov process, and, in the mean square sense, is uniquely determined by the initial condition x_{t_0}.

Let $Q(t)$ be defined as

$$E\{d\beta_t\, d\beta_t^T\} = Q(t)\, dt,$$

then the probability density function $p(x, t)$ of x_t is the solution of the Fokker-Plank-Kolmogorov equation

$$\frac{\partial p}{\partial t} = -\sum_1^n \frac{\partial(pf_i)}{\partial x_i} + \frac{1}{2} \sum_{i,j=1}^n \frac{\partial^2[p(GQG^T)_{ij}]}{\partial x_i\ \partial x_j}\,. \tag{4.4}$$

4.3. *Application to distributed models of populations*

The main idea is the following: by using a simple difference scheme, Eq. (2.8a) is reduced to a system of ordinary differential equations for which it is possible to build up a stochastic model similar to Eq. (4.1). And then, by letting the discretization span tend to zero in the latter, we can arrive at a stochastic distributed model. So, we proceed as follows.

(*Step* 1) For the sake of simplicity, we rewrite Eq. (2.8a) in the form

$$\dot{x}(t, z) = L(x; t, z)$$

where $L(\cdot; t, z)$ denotes the operator of the right-hand side.

This being so, we define a distributed Brownian motion $\beta_t(z)$ with the property that $\beta_t(z)$ and $\beta_t(s)$ are independent for every pair (z, s); and with unit variance parameter.

With these notations, the most direct stochastic version of Eq. (2.8a) is

$$dx_t(z) = L(x; t, z) + H(x; t, z) \int_0^Z g(x; t, z, s)\, d\beta_t(s), \tag{4.5}$$

where H denotes a functional of $\{x_t(z), 0 \le z \le Z\}$, and g is a function of $x_t(z)$.

Given these notations, the generalization of Ito's theory should apply with the norms

$$|\, x(z)\, | := (\int_0^Z x^2\,(z)\, dz)^{1/2} \tag{4.6}$$

and

$$|\, g(z, s)\, | := (\int_0^Z \int_0^Z g^2(z, s)\, dz\, ds)^{1/2}. \tag{4.7}$$

(*Step* 2) The problem now is the one of determining the explicit expressions of $H(x; t, z)$ and $g(x; t, z, s)$.

At first glance, the effect of the random disturbance is to introduce random fluctuations on the coefficients a, b, and r themselves, and a global approach to modelling this feature consists in putting

$$H(x; t, z) \equiv L(x; t, z).$$

This being so, as the dependence of the random noise upon x is already taken into account by H, we can restrict the study to the case in which g is independent of x; and if we consider a stationary disturbance, we then obtain the final model in the explicit form

$$\begin{aligned} dx_t(z) = {} & [1 + \int_0^Z g(z, s)\, d\beta_t(s)]\{\int_0^Z a(t, z, s)x_t(s)\, ds \\ & - [b(t, z) + \int_0^Z r(t, z, s)x_t(s)\, ds]x_t(z)\}. \end{aligned} \tag{4.8}$$

With the engineering notation, we shall introduce the zero-mean white Gaussian noise process

$$w_t(s) := d\beta_t(s)/\, dt \tag{4.9}$$

with

$$E\{w_t(z)w_\tau(s)\} = q(t, z, s)\delta(t - \tau), \tag{4.10}$$

therefore the equation

$$\begin{aligned} \dot{x}_t(z) = {} & [1 + \int_0^Z g(z, s)w_t(s)\, ds]\{\int_0^Z a(t, z, s)x_t(s)\, ds \\ & - [b(t, z) + \int_0^Z r(t, z, s)x_t(s)\, ds]x_t(z). \end{aligned} \tag{4.11}$$

The covariance function $q(t, z, s)\delta(t - \tau)$ has a sharp maximum at $z = s$, and for instance, one may have

$$q(t, z, s) = q_0(t)\frac{\sin \omega(z - s)}{z - s}$$

5. COMPARISON WITH PREVIOUS MODELLING

5.1. *Hutchinson's model*

One of the by now most widely accepted models is the following equation introduced by Hutchinson[7], which is

$$\dot{N}(t) = k[1 - N(t - \tau)K]N(t), \tag{5.1}$$

to describe the growth of a single species population of size N, where k denotes the net reproductive rate, K denotes the carrying capacity, and τ is a time-lag which represents the average recovery time of resources. This equation may be derived as follows.

The population size $x(t, z)$ between ages z and $z + dz$ is ruled by the transport equation

$$\frac{\partial x}{\partial t} + \frac{\partial x}{\partial z} = -\mu(t, z)x, \tag{5.2}$$

with the boundary condition (2.9a). If we assume[8] that (i) there is a stable age distribution, (ii) the birth rate per individual is a constant a_0, and (iii) μ is dependent upon the total number of individuals which compete for food at time τ earlier, we can then write μ in the form

$$\mu = \bar{b} + (\bar{a} - \bar{b})N(t - \tau)/K, \tag{5.3}$$

where $\bar{a}$, $\bar{b}$, and K denote three constants.

Next, the total population $N(t)$ is

$$N(t) = \int_0^\infty x(t, z)\, dz, \tag{5.4}$$

and on integrating Eq. (5.2), we obtain

$$\dot{N}(t) = a_0\hat{N}(t) - \mu N(t), \tag{5.5}$$

where $\hat{N}(t)$ is defined as

$$\hat{N}(t) = \int_0^Z x(t, z)\, dz. \tag{5.6}$$

According to the assumptions, one has

$$\hat{N}(t) = fN, f = \text{constant}. \tag{5.7}$$

If we define $\bar{a}$ as the effective birth rate, such that

$$\bar{a} = fa_0, \tag{5.8}$$

then Eq. (5.5) takes the final form

$$\dot{N} = (\bar{a} - \bar{b})N(t)[1 - N(t - \tau)/K], \tag{5.9}$$

which is equivalent to (5.1) on putting $k := \bar{a} - \bar{b}$.

5.2. *Comparison with the distributed model*

By comparing Eqs. (3.2a) and (4.3), we have the identification

$$\bar{b} + (\bar{a} - \bar{b})N(t - \tau)/K \approx b(t, z) + \int_0^Z r(t, z, s)x(t - \tau, s)\, ds. \tag{5.10}$$

The averaging theorem for integrals yields

$$\int_0^Z r(t, z, s)x(t - \tau, s)\, ds = \bar{r}(t, z)N(t - \tau). \tag{5.11}$$

Therefore, we obtain

$$\bar{b} + (\bar{a} - \bar{b})N(t - \tau)/K \approx b(t, z) + \bar{r}(t, z)N(t - \tau), \tag{5.12}$$

therefore

$$\bar{b} \approx b(t, z) \tag{5.13}$$

$$(\bar{a} - \bar{b})/K \approx \bar{r}(t, z). \tag{5.14}$$

According to Eq. (5.13), $\bar{b}$ can be thought of as an averaging value for $b(t, z)$, for instance

$$\bar{b} = \frac{1}{TZ} \int_0^T \int_0^Z b(t, s)\, dt\, ds,$$

where T denotes a given horizon. Likewise, one may set

$$\frac{\bar{a} - \bar{b}}{K} = \frac{1}{TZ} \int_0^T \int_0^Z \bar{r}(t, s)\, dt\, ds.$$

6. STATIONARY SOLUTION OF MODEL 2.7

Our purpose in the present section is to obtain an estimate for the steady-state solutions (different from the zero trivial one) of the deterministic model defined by Eq. (2.7), given some simplifying conditions.

6.1. *A prerequisite class of sufficient conditions*

6.1.1. *Assumptions.* For the sake of mathematical consistency, we shall assume that the coefficients $a(t, z, s)$, $b(t, z)$, and $w(t, z, s)$ are continuous functions of their arguments, and that $a(t, z, s) > 0$, $b(t, z) > 0$. We shall further assume that $r(t, z, s) \neq 0$; $r(t, z, s) > 0$ represents intra-species competitions, while $r(t, z, s) < 0$ defines mutual assistance.

6.1.2. *Sufficient conditions for the existence of a stationary state $x(z)$.* According to Eq. (2.7a), such a $x^*(z)$, if there is any, is given by the expression

$$x^*(z) = \frac{\displaystyle\int_0^Z a(t, z, s)x^*(s)\, ds}{b(t, z) + \displaystyle\int_0^Z r(t, z, s)x^*(s)\, ds} \tag{6.1a}$$

$$=: P(t, z)/Q(t, z), \tag{6.1b}$$

where the symbol $=:$ means that the right-hand side term is defined by the left-hand side one, while $:=$ signify that the left-hand side is defined by the right-hand side one.

But since $P(\cdot)/Q(\cdot)$ is time unvarying, its time derivative is zero, therefore the condition

$$\frac{\dot{P}(t, z)}{P(t, z)} - \frac{\dot{Q}(t, z)}{Q(t, z)} = 0.$$

There is then a constant λ such that

$$\dot{P}/P = \dot{Q}/Q = \lambda.$$

Integrating with respect to P yields the necessary condition

$$\int_0^Z a(t, z, s)x^*(s)\,\mathrm{d}s = e^{\lambda t} \int_0^Z a(0, z, s)x^*(s)\,\mathrm{d}s, \tag{6.2}$$

therefore, the sufficient condition

$$a(t, z, s) = a(0, z, s)e^{\lambda t}. \tag{6.3}$$

Likewise, integrating *w.r.t* Q yields the necessary condition

$$Q(t, z) = Q(0, z)e^{\lambda t}, \tag{6.4}$$

therefore, the sufficient conditions

$$b(t, z) = b(0, z)e^{\lambda t} \tag{6.5}$$

$$r(t, z, s) = r(0, z, s)e^{\lambda t}. \tag{6.6}$$

Conditions (6.3), (6.5), and (6.6) are sufficient conditions in order that Eq. (2.7a) have a time-independent solution.

6.2. *A class of sufficient conditions*

We shall obtain an approximate sufficient condition for the existence of $x^*(z)$ by considering the total population

$$N := \int_0^Z x(s)\,\mathrm{d}s.$$

The rationale is that if N exists and is bounded, then it is so for $x(z)$.

To this end, we use the sufficient conditions (6.3), (6.5), and (6.6) to rewrite Eq. (2.7a) in the form

$$\int_0^Z a(0, z, s)x^*(s)\,\mathrm{d}s = [b(0, z) + \int_0^Z r(0, z, s)x(s)\,\mathrm{d}s]x^*(z). \tag{6.7}$$

We integrate over $[0, Z]$ and we apply the mean value theorem for integrals to obtain

$$a(0, z_1, s_1)N = b(0, s_2)N + r(0, z_3, s_3)N^2, \tag{6.8}$$

with $0 < z_1, s_1, s_2, z_3, s_3 < Z$. We then have

$$N = \frac{a(0, z_1, s_1) - b(0, s_2)}{r(0, z_3, s_3)}. \tag{6.9}$$

Despite the fact that the exact values of these s_i and z_i's are not known, we can state the following result.

PROPOSITION 1. Assume that the sufficient conditions (6.3), (6.5), and (6.6) are satisfied.

(i) A sufficient condition in order that the system (2.7a) with intra-species competition, that is to say with $w(t, z, s) > 0$, have a non-trivial time unvarying solution, is

$$\min_{s,z} a(0, z, s) > \max_{z} b(0, z). \tag{6.10}$$

(ii) For the system with mutual assistance, $w(t, z, s) < 0$, and a sufficient condition for the existence of a time-independent solution is

$$\max_{z,s} a(0, z, s) < \min_{z} b(0, z). \tag{6.11}$$

6.3. *Expression of the stationary solutions*

By taking account of the necessary conditions (6.3), (6.5), and (6.6), Eq. (6.1) yields

$$x^*(z) = \frac{\int_0^Z a(0, z, s)x^*(s)\, \mathrm{d}s}{b(0, z) + \int_0^Z r(0, z, s)x^*(s)\, \mathrm{d}s}, \tag{6.12}$$

and by using the mean value theorem for integrals, we find that there are two constants $k_1 := x(s_1)$ and $k_2 := x(s_2)$ such that

$$x^*(z) = \frac{k_1 \int_0^Z a(0, z, s)\, \mathrm{d}s}{b(0, z) + k_2 \int_0^Z r(0, z, s)\, \mathrm{d}s}. \tag{6.13}$$

This expression (6.13) is an estimate which gives indications on the structure and the qualitative behaviour of the steady-state solution $x^*(z)$.

6.4. *A few theoretical considerations*

We may write Eq. (6.2) in the form

$$\int_0^Z [a(t, z, s) - e^{\lambda t}a(0, z, s)]x^*(s)\, \mathrm{d}s = 0, \tag{6.14}$$

which is an integral equation. If we denote by $D_a(\lambda, t)$ its Fredholm determinant, then a necessary condition in order that it has a solution different from the trivial one is

$$D_a(\lambda, t) = 0 \text{ for every } t. \tag{6.15}$$

Likewise, one should have

$$\int_0^Z [r(t, z, s) - e^{\lambda t}r(0, z, s)]x^*(s)\, \mathrm{d}s = -[b(t, z) + b(0, z)e^{\lambda t}],$$

therefore

$$x^*(s) = -\int_0^Z [b(t, z) + b(0, z)e^{\lambda t}] \frac{D_r(z, s; \lambda, t)}{D_r(\lambda, t)} \, ds, \tag{6.16}$$

where $D_r(z, s; \lambda, t)$ and $D_r(\lambda, t)$ denote the corresponding Fredholm determinants.

The solution (6.16) should simultaneously satisfy (6.14) with additional conditions to ensure the independent upon t.

These remarks justify the need of approximate conditions simpler to use from a practical standpoint, therefore the Eqs. (6.3)–(6.6).

We point out that these conditions are not as restrictive as they look at first glance. First $\lambda = 0$ corresponds to the important case where the different coefficients in question are constant. Second, from a phenomenological standpoint, they mean that $a(t, z, s)$, $b(t, z)$, and $r(t, z, s)$ would satisfy the equation

$$\dot{y}(t, z, s) = \lambda y(t, z, s),$$

which would then look like the dynamics of the internal structure of the population under consideration, which is quite meaningful.

We shall also point out that it is sufficient that conditions (6.3)–(6.6) by asymptotically satisfied to have the asymptotic steady state.

6.5. *Numerical considerations*

Expression (6.9) by itself may serve as an initial approximation to numerically determine $x^*(z)$. Indeed, on substituting (6.9) into (2.7) we get a residual term $\epsilon(k_1, k_2)$; and (k_1, k_2) will be selected in order to minimize $\epsilon(k_1, k_2)$; which can be done numerically, for instance, by using the gradient technique. This is nothing else but the Gaberkin method suitably applied to our problem.

As in evidence, the sufficient condition (6.10) is a bit restrictive, and it remains, of course, to determine more general conditions for the existence of the steady state $x^*(z)$.

By using a simple difference scheme, we reduced Eq. (2.8) to a set of ordinary differential equations. More explicitly, we put

$$x_i := \int_{z_{i-1}}^{z_i} x(t, s) \, ds.$$

to obtain

$$\dot{x}_i = \sum_j a_{ij} x_j - (b_i + \sum_j r_{ij} x_j) x_i; \qquad i = 1, 2, \ldots, n$$

with the initial condition

$$x_i(0) = x_{i0} = \int_{z_{i-1}}^{z_i} x_0(s) \, ds,$$

and we solved the corresponding Cauchy problem.

The computation shows that if the difference

$$R(z) := \max_s r(z, s) - \min_s r(z, s)$$

is sufficiently large, then, independently of the initial distribution, there is a limiting distribution whose the dispersion is inversely proportional to the value of $R(z)$.

The condition $R(z)$ large may be considered as representing a rigorous selection. If we further assume that $r(z, s)$ characterizes the adapting properties of the individuals to their environment in the presence of limited resources, this simulation would illustrate a natural selection of the Darwinian class.

7. STATIONARY SOLUTIONS OF MODEL (2.10)

7.1. *Preliminary remarks*

We shall denote by $x'(s)$ the derivative $\mathrm{d}x(z)/\,\mathrm{d}z$.

7.1.1. *Assumptions.* They concern the coefficients $a(t, s)$, $b(t, z)$, and $w(t, z, s)$ and they are similar to the assumptions in subsection (6.1) above.

7.1.2. *Sufficient conditions.* According to Eq. (2.10), the stationary solution $x^*(z)$ is defined by the equation

$$\frac{x^{*\prime}(z)}{x^*(z)} = -b(t, z) - \int_0^Z r(t, z, s)x^*(s)\,\mathrm{d}s, \tag{7.1}$$

with the boundary condition (2.9a), which yields

$$x(0) = \int_0^Z a(t, s)x^*(s)\,\mathrm{d}s. \tag{7.2}$$

It follows that sufficient conditions for the existence of stationary solutions are the trivial ones, say

$$a(t, z) = a(z);\ b(t, z) = b(z);\ r(t, z, p) = r(z, s), \tag{7.3}$$

independent of time.

7.2. *The homogeneous boundary problem*

If we assume that $r(z, s) = 0$, we then have a homogeneous boundary problem for which Fredholm's alternative holds: either the system does not have any stationary solution different from zero, or there is an infinite set of possible stationary solutions, which occur when some combination of the parameters involved by the system is equal to the eigenvalue of the linear operator, and when the evolutionary operator has a unique eigenvalue

$$\nu := \int_0^Z a(s)\exp[-\int_0^z b(s)\,\mathrm{d}s\,\mathrm{d}z \tag{7.4a}$$

$$= 1. \tag{7.4b}$$

It is, therefore, of interest to analyze the influence of the *structural parameter* ν on the behaviour of the nonlinear system (2.10).

7.3. *Stationary state of the nonlinear model*

Equation (7.1) together with condition (7.4) yields

$$x^*(z) = x(0)\exp[-\int_0^z b(s)\,ds - \int_0^z dy \int_0^Z r(y, s)x(s)\,ds], \tag{7.5}$$

and we substitute this expression into the boundary condition (7.2) to obtain the closed loop condition for the existence of a nontrivial steady state, in the form

$$\int_0^Z a(z)\exp[-\int_0^z b(s)\,ds]\exp[-\int_0^z dy\int_0^Z r(y, s)x(s)\,ds]\,dz = 1. \tag{7.6}$$

We now apply the mean value theorem for integrals, so that there is a ξ, $0 < \xi < Z$ such that

$$\exp[-\int_0^\xi dy\int_0^Z r(y, s)x(s)\,ds] = \frac{1}{\nu}. \tag{7.7}$$

But according to the conditions $r(z, s) > 0$ and $x^*(z) \geq 0$ and $x^*(z) \geq 0$, the left-hand side term of this equation is smaller than the unity, so that (7.7) is not always satisfied, and two cases are to be considered depending upon whether $\nu > 1$ or $\nu < 1$.

(i) Assume that $r(z, s) > 0$ and $\nu > 1$. Then Eq. (2.10) has two stationary states: the trivial one zero and the nontrivial one referred to as $x^*(z)$. Moreover, it is a simple matter, for instance by considering the total population N, to show that only the state $x^*(z)$ is stable.

(ii) Assume that $r(z, s) > 0$ and $\nu < 1$. Then Eq. (7.7) cannot be satisfied, and the only stationary solution is the trivial one, and it is moreover stable; in other words, the population is doomed to extinction.

(iii The case $r(z, s) < 0$, that is to say the mutual assistance is exactly the opposite one. When $\nu > 0$, the only stationary solution is the trivial one and $\nu < 1$ defines two steady-states: the trivial one and $x^*(z)$.

In both cases, $\nu = 1$ is a bifurcation point.

7.4. *Expression of the stationary solution*

According to Eq. (7.5), on applying the mean value theorem for integrals, there is a constant $k_3 := x(s_3)$ such that

$$x^*(z) = x(0)\exp[-\int_0^z b(s)\,ds - k_3\int_0^z dy\int_0^Z r(y, s)\,ds]. \tag{7.8}$$

8. ANALYSIS OF THE STOCHASTIC MODEL

8.1. *The general feature of the approach*

Our main purpose in this section is to get an estimate of how the stationary state $x^*(z)$ is affected by the presence of the random noise $w_t(s)$, and to this end, we shall use approximate techniques.

(i) First, we shall linearize the system around the stationary solution to get an equation of the deviation from $x^*(z)$.

(ii) Second, the linear equation so obtained is only an integral equation with respect to the distributed parameter z, so that by using the well-known technique initiated by Fredholm, it will be possible to extend the results related to linear multivariable stochastic differential equations (see, for instance, [9]).

8.2. *Equation of the deviation from* $x^*(z)$

We define the deviation $y_t(z)$ by the equation

$$x_t(z) =: x^*(z) + y_t(z), \tag{8.1}$$

and we employ the approximation

$$f(x_t) \cong f(x^*) + f'_x(x^*)y_t(z). \tag{8.2}$$

By using a direct calculation, equation (4.11) yields

$$\begin{aligned}\dot{y}_t(z) = &\int_0^Z [a(t, z, s) - x^*(z)r(t.z.s)]y_t(s)\,ds \\ &- [b(t, z) + \int_0^Z r(t.z.s)x^*(s)\,ds]y_t(z) + L(x^*, t, z)\int_0^Z g(z, s)w_t(s)\,ds.\end{aligned} \tag{8.3}$$

Let $\hat{y}_t(z)$ denote the statistical average $E\{y_t(z)\}$; then, taking the expectation of both sides of Eq. (8.3) direct yields

$$\begin{aligned}\dot{\hat{y}}_t(z = &\int_0^Z [a(t, z, s) - x^*(z)r(t, z, s)]\hat{y}_t(s)\,ds \\ &- [b(t, z)) + \int_0^Z r(t, z, s)x^*(s)\,ds]\hat{y}_t(z).\end{aligned} \tag{8.4}$$

According to Section (6.1), if there is a stationary solution $x^*(z)$, then this may be caused by the conditions (6.3)–(6.6); and then the stationary average $\hat{y}(z)$ is given by the equation

$$\hat{y}(z) = \frac{\displaystyle\int_0^Z a(0, z, s)\hat{y}(s)\,ds - x^*(z)\int_0^Z r(0, z, s)\hat{y}(s)\,ds}{\displaystyle b(0, z) + \int_0^Z r(0, z, s)x^*(s)\,ds}. \tag{8.5}$$

By virtue of the mean value theorem for integrals, there are two constants k_4 and k_5 such that

$$\hat{y}(z) = \frac{\displaystyle k_3\int_0^Z a(0, z, s)\,ds - k_4x^*(z)\int_0^Z r(0, z, s)\,ds}{\displaystyle b(0, z) + \int_0^Z r(0, z, s)x^*(s)\,ds}. \tag{8.6}$$

This expression (8.6) provides a picture of $\hat{y}(z)$ and could serve as a point of departure to solve (8.5) numerically.

8.2. *Covariance equation of the deviation*

We define the covariance function

$$P(t, z, s):= E\{[y_t(z) - \hat{y}_t(z)][y_t(s) - \hat{y}_t(s)]\} =: E\{\Delta y_t(z)\Delta y_t(s)\} \tag{8.7}$$

and our purpose now is to obtain its differential equation. For the sake of simplicity, we shall introduce the linear operator $F(y, t, z)$ and we shall put

$$h(t, z) := L(x^*, t, z), \tag{8.8}$$

to rewrite Eq. (8.3) in the form

$$\dot{y}_t(z) = F(y_t, t, z) + h(t, z)\int_0^Z g(z, s)w_t(s)\,ds, \tag{8.9}$$

where the meaning of $F(\cdot)$ is obvious. We further recall that linear stochastic differential equations can be manipulated by formal rules, and we shall use this possibility here, via the discretization technique of Fredholm.

8.2.1. *Formal expression of* $y_t(z)$. The solution of (8.9) is

$$y_t(z) = \int_0^Z \phi(z, s, t, 0)y_0(s)\,ds + \int_0^t\int_0^Z \phi(z, s, t, \tau)h(t, z)g(z, s)w_\tau(s)\,d\tau\,ds, \tag{8.10}$$

where $\phi(z, s, t, \tau)$, with $\phi(z, s, t, t) = 1$, is the solving kernel, (that is to say, the infinite dimensional form of the state transition matrix in linear systems) of the homogeneous equation

$$\dot{y}_t(z) = F(y_t, t, z).$$

Taking the expectation in (8.10) we get

$$\hat{y}_t(z) = \int_0^Z \phi(z, s, t, 0)y_0(s)\,ds, \tag{8.11}$$

which is Eq. (8.4).

8.2.2. *Derivation of the covariance equation.* One has (the notation $\dot{\overline{\Delta y_t}}$ holds for $\partial\Delta y_t/\partial t$)

$$\dot{P}(t, z, s) = E\{\dot{\overline{\Delta y_t}}(z)\Delta y_t(s)\} + E\{\dot{\overline{\Delta y_t}}(z)\,\Delta y_t(s)\}. \tag{8.12}$$

From (8.4) and (8.9), we have

$$\dot{\overline{\Delta y_t}}(z) = F(\Delta y_t, t, z) + h(t, z)\int_0^Z g(z, s)w_t(s)\,ds, \tag{8.13}$$

so that

$$\begin{aligned}\dot{P}(t, z, s) &= F[P(t, z, \xi), t, s] + E\{\Delta y_t(z)h(t, s) \int_0^Z g(s, \xi)w_t(\xi)\, d\xi\} \\ &\quad + F[P(t, s, \xi), t, z] + E\{\Delta y_t(s)h(t, z) \int_0^Z g(s, \xi)w_t(\xi)\, d\xi\}.\end{aligned} \tag{8.14}$$

Now

$$\begin{aligned}E\{\Delta y_t(s) \int_0^Z h(t, z)g(z, \xi)w_t(\xi)\, d\xi\} &= E\{[\int_0^Z \phi(s, \xi, t, 0)[y_0(\xi) - \hat{y}_0(\xi)]\, d\xi \\ &\quad + \int_0^t \int_0^Z \phi(s, \eta, t, \tau)h(t, s)g(s, \eta)w_\tau(\eta)\, d\eta\, d\tau] \\ &\quad \times \int_0^Z h(t, z)g(z, \xi)w_t(\xi)\, d\xi\} \\ &= \int_0^t \int_0^Z \int_0^Z \phi(s, \eta, t, \tau)h(t, s)h(t, z) \\ &\quad \times g(s, \eta)g(z, \xi)q(t, \xi, \eta)\delta(t - \tau)\, d\eta\, d\xi\, d\tau \\ &= \tfrac{1}{2} \int_0^Z \int_0^Z h(t, s)h(t, z)g(s, \eta)g(z, \xi)q(t, \xi, \eta)\, d\xi\, d\eta.\end{aligned} \tag{8.15}$$

The calculation of

$$E\{\Delta y_t(z) \int_0^Z h(t, s)g(s, \xi)w_t(\xi)\, d\xi\} \tag{8.16}$$

provides the same expression.

On substituting these results into Eq. (8.14), we finally obtain

$$\begin{aligned}\dot{P}(t, z, s) &= \int_0^Z A(t, s, \xi)P(t, z, \xi)\, d\xi + \int_0^Z A(t, z, \xi)P(t, s, \xi)\, d\xi \\ &\quad - [b(t, s) + B(t, s)]P(t, z, s) \\ &\quad - [b(t, z) + B(t, z)]P(t, s, z) \\ &\quad + W(\mathrm{t, z, s}),\end{aligned} \tag{8.17}$$

with the notations

$$A(t, z, \xi) := a(t, z, \xi) - x^*(z)r(t, z, \xi) \tag{8.18}$$

$$B(t, z) := \int_0^Z r(t, z, \xi)x^*(\xi)\, d\xi \tag{8.19}$$

$$W(t, z, s) := \int_0^Z \int_0^Z h(t, z)h(t, s)g(s, \eta)g(z, \xi)q(t, \xi, \eta)\, d\xi\, d\eta. \tag{8.20}$$

8.3. *Local covariance $P(t, z, z)$*

In order to get an estimate of $P(t, z, z)$, we shall assume that the latter has a sharp value at $z = s$ so that we can neglect its contribution as soon as $| z - s | \geq \epsilon$. Under these conditions, Eq. (8.17) yields

$$\dot{P}(t, z, z) \cong 2[\epsilon A(t, z, z) - B(t, z) - b(t, z)]P(t, z, z) + W(t, z, z). \tag{8.21}$$

According to Section 6.1, we consider the special case where the conditions (6.3)–(6.6) are satisfied, therefore one has

$$h(t, z) = e^{\lambda t}h(0, z).$$

So, on assuming that $q(t, z, \xi)$ is independent of t, we can write Eq. (8.21) in the form

$$\dot{P}(t, z, z) \cong e^{\lambda t}C(z, \epsilon)P(t, z, z)e^{2\lambda t}W(z, z), \tag{8.22}$$

with the notation

$$e^{\lambda t}C(z, \epsilon) := 2[\epsilon A(t, z, z) - B(t, z) - b(t, z)] \tag{8.23}$$

$$e^{\lambda t}W(z, s) := W(t, z, s). \tag{8.24}$$

In the special case where $\lambda = 0$, the stationary covariance $P(z, z)$ is

$$P(z, z) \simeq \frac{W(z, z)}{2[b(z) + B(z) - \epsilon A(z, z)]} \tag{8.25}$$

9. CONCLUDING REMARKS

9.1.1. *Outline of a soci-economic example.* In the introduction we claimed that the motivation of the present work is the necessity that exists, in some cases, to have the exact distribution of the population rather than its global value, and the following is an example of such a situation.

Assume that $x(t, z)$ is the distribution of the gross national product of a country, and that z characterizes the population, for instance z may be the income. A part of the national product is reinvested; this is the term $a(t, z, s)x(t, s)$ in Eq. (2.8). A second part is directly utilized as current expenditures of the government (civil servants, transportation, etc.), and is represented by the term $b(t, z)x(t, z)$ in Eq. (2.8). A third part consists of the social expenditures of the government which are of paramount importance in our western democracies; they result directly from social struggles in the country, and they are represented by the competition term $t(t, z, s)x(t, s)$ in Eq. (2.8). In such a condition, it is of interest to have the exact distribution of the national income among the population and to have a distributed estimate of the discouraging effects of the income tax levels on the production.

9.1.2. *On the stochastic modelling.* We have applied a practical approach of standard use in engineering and physics to describe the stochastic model, and this viewpoint is justified as far as any numerical computation works on a finite dimensional system only. An obvious limitation of the linearization technique is the confinement of the trajectory close to the steady state solution; for large deviations from this value, the problem is fully nonlinear and numerical solution would be required.

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